

Decomposition patterns, nutrient availability, species identities and vegetation changes in central-European summit bogs

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The global increase in atmospheric nitrogen deposition leads to changes in decomposition activity, which has been observed especially in nutrient-limited bog ecosystems relying on atmospheric inputs as the sole source of external nutrients. We conducted a reciprocal transplant decomposition experiment in two bogs in central Europe to test the effects of *Sphagnum* species (*S. fallax*, *S. magellanicum*, *S. rubellum/russowii*, cellulose strips as controls), material origin and the environment on *Sphagnum* decomposition and related nutrient release. Cellulose, but not *Sphagnum* biomass, decomposed more rapidly in the warmer and nitrogen-rich conditions of the suboceanic Jizera Mts. than in the subcontinental Jeseníky Mts. In the *Sphagnum* biomass transplants, interspecific differences in decomposition overruled the effects of both the origin of the material and the environment of the decomposition site, with *S. magellanicum* decomposing the slowest. Possible relationships between decomposition rates and recent changes in *Sphagnum* species composition in N-polluted bogs are discussed.

Introduction

Peatlands are one of the largest and most threatened global reservoirs of carbon (C). Due to their specific conditions, such as permanent waterlogging, cold climate, shortage of nutrients and slower plant tissue decomposability accompanied by low microbial activity, peatlands

store dead organic matter. However, allogenic environmental changes disrupt the equilibrium between peat accumulation and peat decomposition (e.g., Franzén 2006, Gunnarsson *et al.* 2008).

Sphagnum mosses dominate the vegetation of ombrotrophic bogs, and their decay-resistant litter makes up the bulk of peat. Decomposition

rates of *Sphagnum* biomass primarily depend on habitat conditions (Belyea 1996, Laiho 2006, Moore *et al.* 2007), litter quality (Johnson and Damman 1991, Turetsky *et al.* 2008, Hájek *et al.* 2011) and microbial activity (Thormann *et al.* 2004, Allison and Treseder 2011). Both the changing climate (drier summer periods, higher mean temperatures) and continuously high nitrogen deposition load in central Europe (Jiroušek *et al.* 2011, Granath *et al.* 2014, Hůnová *et al.* 2014) are supposed to enhance decomposition processes and thus carbon loss in bogs. These processes may become even more apparent when temperatures and N deposition increase synergistically (Berendse *et al.* 2001, Bragazza *et al.* 2006, Limpens *et al.* 2011). Hitherto, no consensus has been reached in the literature regarding the impacts of N on *Sphagnum* decomposition. Fertilisation experiments (Aerts *et al.* 2001, Limpens and Berendse 2003, Bubier *et al.* 2007, Gerdol *et al.* 2007, Bragazza *et al.* 2012), a large-scale transplant experiment (Breeuwer *et al.* 2008) and a comparative study (Bragazza *et al.* 2006) found N to have a positive or no effect on *Sphagnum* decomposition. Turetsky *et al.* (2008) even found a negative relationship between the concentration of N in *Sphagnum* biomass and its decomposition rate. These discrepancies across studies focused on the effects of global change on *Sphagnum* decomposition might be caused not only by different methodologies, but also by differences in the initial chemistry of *Sphagnum* biomass, different background environmental conditions, duration of decomposition experiments or different species identity.

Recent studies focused on bog ecosystems in the context of ongoing global climate changes and alterations of nutrient cycles generally treat the entire genus *Sphagnum* as a single functional group (Bragazza *et al.* 2005a, 2006, 2008, Bragazza and Freeman 2007, Gerdol *et al.* 2007, Straková *et al.* 2012). Decomposition rates of different *Sphagnum* species have long been known to differ, however (Clymo 1965, Moore *et al.* 2007: table 6). Interspecific differences in *Sphagnum* decomposition have so far been studied predominantly in the context of explaining bog microtopography (Johnson and Damman 1991, Hájek 2009), as hummock species are known

to decay slower than lawn and hollow species (Belyea 1996, Limpens and Berendse 2003, Turetsky *et al.* 2008). Besides decomposition experiments using native *Sphagnum* material, cellulose tests can be carried out to determine the decomposition rate of standard material not affected by the chemical properties of *Sphagnum* material (Bartsch and Moore 1985, Braekke and Finér 1990, Hájek 2009). Although cellulose tests have limited relevance in bogs, because bog fungi specifically degrade particular compounds forming *Sphagnum* tissues (Domsch *et al.* 1980, Thormann *et al.* 2001, 2002, Moore *et al.* 2007), cellulose is a useful standardized substrate for demonstrating the effects of environmental conditions on rates of decomposition.

We established a transplant experiment in two regions of the Sudetes Mts. in central Europe that differ in local climate, N deposition and nutrient availability, resulting in different nutrient concentrations and stoichiometry (N:P and N:K ratios) in *Sphagnum* material (Jiroušek *et al.* 2011). We thus aimed to test the importance of the separate effects of (i) species identity, (ii) the origin of material, and (iii) the environment at decomposition sites on cellulose and *Sphagnum* mass loss and related nutrient release.

Material and methods

Study sites

The experiment was carried out in two ombrotrophic mountain bogs in the Sudetes (border region between Czech Republic and Poland): Jizerka in the Jizera Mts. (50°49'38"N, 15°19'40"E, 870 m a.s.l.) and Vozka in the Jeseníky Mts. (50°09'32"N, 17°06'25"E, 1320 m a.s.l.). The distance between these sites is about 150 km. The two regions differ in their climate, nutrient conditions and N deposition load (Jiroušek *et al.* 2011). The westward located Jizera Mts. are characterised by a suboceanic climate with higher temperatures, a more uniform course of precipitation during the year and a longer vegetation period. The subcontinental Jeseníky Mts. reach higher elevations and are about 2 °C colder than the Jizera Mts. (Fig. 1a). The weather during the field experiment cor-

responded to long-term conditions without any exceptional fluctuations.

In the long-term, the mean water level in lawns is similar in both regions, about -12 cm in the Jizera Mts. and about -15 cm in the Jeseníky Mts. This small difference is caused by especially the more pronounced water level decrease in the subcontinental Jeseníky Mts. in drier periods, which did not occur during the experiment (Fig. 1b). The water regime in both regions has not been altered by human interventions.

Rates of N deposition in both study regions are high as compared with those in other areas of Europe, with higher long-term values (about $2\text{--}2.5\text{ g m}^{-2}\text{ year}^{-1}$ over 3 years prior to the experiment) in the Jizera Mts. as compared with those ($1.25\text{ g m}^{-2}\text{ year}^{-1}$) in the Jeseníky Mts. (Bragazza *et al.* 2004, Jiroušek *et al.* 2011). Because of high precipitation, wet deposition predominates, and the proportion of nitrates and ammonium is approximately comparable (Hájková *et al.* 2011). In the Jizera Mts, the maximum peat depth of bogs is about 450 cm. The maximum peat depth of the study bog in the Jeseníky Mts. is 165 cm, and its age dates back 6000 years (Dudová *et al.* 2013).

The vegetation at the Jeseníky Mts. site is more homogeneous and relatively species-poor as compared with that at the Jizera Mts. site. Lawns and low hummocks at the Jeseníky Mts. site are formed by the peat mosses *Sphagnum angustifolium*, *S. fallax*, *S. magellanicum* and *S. russowii*, and are covered by *Eriophorum vaginatum* and the dwarf shrubs *Andromeda polifolia*, *Calluna vulgaris*, *Empetrum hermaphroditum*, *Vaccinium oxycoccos* and *V. uliginosum*. At the margins, the bogs gradually transition into peat spruce forests. The vegetation at the Jizera Mts. site is more heterogeneous because of the occurrence of *Sphagnum papillosum*, *S. tenellum*, *Trichophorum cespitosum* and other sub-oceanic plant species that are absent from the Jeseníky Mts. Lawns and low hummocks are formed predominantly by *S. fallax*, *S. magellanicum*, *S. papillosum* and *S. rubellum*, with the presence of *Eriophorum vaginatum*, *Trichophorum cespitosum* and dwarf ericoid shrubs. Higher hummocks are formed by *Sphagnum fuscum* and *S. rubellum*, and occur only at the eastern edge of the bog. The whole perimeter of

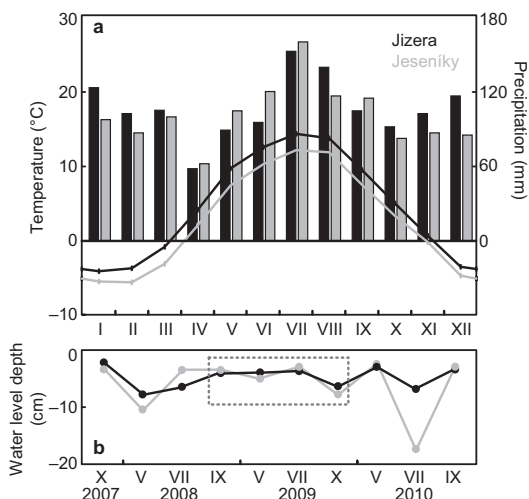


Fig. 1. (a) Monthly mean temperatures (lines) and precipitation (columns) in the suboceanic Jizera Mts. (black) and the subcontinental Jeseníky Mts. (grey). The data are averages for 10 years prior to the experiment. The data are from meteorological stations of the Czech Hydrometeorological Institute at Kořenov-Jizerka (Jizera Mts.) and Dlouhé stráně (Jeseníky Mts.). (b) Water level fluctuations in permanent holes located in analogous lawn vegetation at both study sites, the Jizera Mts. site (black line) and the Jeseníky Mts. site (grey line). The rectangle marks the time interval of the decomposition experiment (autumn 2008–autumn 2009).

the bog is covered by dwarf pine (*Pinus mugo*).

The nomenclature follows Danihelka *et al.* (2012) for vascular plants and Kučera *et al.* (2012) for bryophytes.

Experimental setup

In August 2008, individuals of dominant *Sphagnum* species (*S. fallax*, *S. magellanicum* and *S. rubellum/russowii*) were collected from low hummocks and lawns at both localities, always in mono-dominant patches with a low cover of vascular plants. These species were chosen because they differ taxonomically and ecologically, and are present in large amounts at both localities. *Sphagnum rubellum* and *S. russowii* are taxonomically allied species with transitional populations observed in the study area. In the suboceanic Jizera Mts., *S. rubellum* occurs in strictly ombrotrophic parts, while in the subcon-

tinental Jeseníky Mts, *S. rubellum* is extremely rare and possibly does not occur in the study bog at all (Hájková *et al.* 2010), *S. russowii* being the dominant species. We therefore refer to *S. rubellum/russowii* in this study, although when interpreting the results, we take into account the taxonomic difference between *S. rubellum* and *S. russowii*.

The material used in the experiments (i.e., live vs. dead, stem vs. capitulum) may affect the results considerably (Limpens and Berendse 2003). *Sphagnum* mosses translocate nutrients from dying to living tissues, especially to the capitula, where metabolic activities are most concentrated (Malmer 1988, Rydin and Clymo 1989, Aldous 2002). The capitula (0–1 cm) were therefore cut off, and only young segments of stems below the capitula (approximately 1–3 cm from the top of the capitulum) were separated and used for the experiments (cf. Bragazza *et al.* 2007, Breeuwer *et al.* 2008, Hájek 2009). Three grammes of oven-dried shoots were sealed inside nylon nets (50 × 150 mm, mesh size 1 mm (Rychnovská and Fiala 1987). An additional part of the material was kept separate for subsequent analytical determination of nutrient concentrations. We prepared mesh bags for each of the three *Sphagnum* species (30 repetitions × 3 species × 2 regions) and 60 mesh bags with cellulose (ash-free filter paper). In October 2008, all mesh bags were placed into the zone with senescent *Sphagnum* stems (~1–6 cm). For each *Sphagnum* species at each bog, we randomly selected five mono-dominant patches, in which we established decomposition experiment sites. Although we tried to avoid the influence of a fluctuating water table by placing mesh bags into drier microhabitats in the case of *S. fallax*, two patches with this species in the suboceanic Jizera Mts. were submerged for part of the year. At each decomposition site, we placed both original and transplanted material from the other locality (three repetitions of both) and cellulose mesh bags as a standard (two repetitions). After one year (in September 2009), all mesh bags were collected and transported to the laboratory. In the laboratory, the biomass was separated from roots and other non-target material, oven-dried and weighed. Finally, the samples were analysed for nutrient and C concentrations.

Nutrient concentration analyses

Dry *Sphagnum* stems were oven-dried to constant weight (at 60 °C) and pulverized before analysis using Retsch planetary ball mill MM 400. Subsequently 10 g of homogenised dry matter was taken for the analytical determination of C, N, phosphorus (P), potassium (K), calcium (Ca) and magnesium (Mg) in 4–5 repetitions for each variant (material origin, *Sphagnum* species). N was determined according to the Kjeldahl method with sulphuric acid and hydrogen peroxide; N concentration was detected by a distillation method with water vapour and sodium hydroxide addition. For determination of the other elements, material was digested in a sealed system with microwave heating. P was detected spectrophotometrically after colouration by a molybdenum agent whereas Ca^{2+} , Mg^{2+} and K^{+} concentrations were determined by flame atomic emission spectrometry and organic C gravimetrically after dry combustion.

Ion-exchange resin analysis

Mineral N was trapped *in situ* by ion exchange resins (IER) inserted into a special cover and IER stockings (Binkley and Matson 1983). These were prepared by placing a mixture of equal proportions of cation- and anion-exchange resin (50% of cation-exchange resin No. Purolite C100E and 50% of anion-exchange resin No. Purolite A520E) in cylindrical stockings (1.5 cm diameter by 10 cm length), made of a fine nylon mesh (grid size of 42 μm). Exchange sites of IER were saturated with Cl^{-} and Na^{+} ions before *in situ* exposition. At each site, 30 IER stockings were installed; two in each microhabitat close to decomposition mesh bags. The ion-exchange resin stockings were deployed *in situ* four times for six months (in May–September 2009, September 2009–May 2010, May–September 2010 and September 2010–May 2011). For the quantification of absorbed $\text{NH}_4^{+}\text{-N}$ and $\text{NO}_3^{-}\text{-N}$ trapped by the resin, the IER were eluted using a solution of 1.7 M NaCl and determined by distillation and titration (Peoples *et al.* 1989). Results from the IER stockings were expressed as mg of $\text{NH}_4^{+}\text{-N}$ per 10 ml IER and $\text{NO}_3^{-}\text{-N}$ per 10 ml IER.

Data analyses

Differences in average mass loss and absorption of N ions by IER were tested using two-way ANOVA followed by Tukey's HSD *post-hoc* test. For the analyses, the data on the mass loss and absorption of N ions by IER were shifted and transformed logarithmically [$\ln(x + 10)$ and $\ln(x + 1)$, respectively] to achieve normality. In the decomposition experiment with cellulose, the following null hypotheses were tested: (1) There is no difference in mass loss between the two environmentally contrasting bogs in the Jizera Mts. and the Jeseníky Mts.; (2) There is no difference in cellulose mass loss among microhabitats characterised by mono-dominant *Sphagnum* species (*S. fallax*, *S. magellanicum* and *S. rubellum/russowii*); and (3) There is no significant interaction between the decomposition site and the microhabitat. Interactions are specified by a combination of particular levels of the two factors in the analysis. An interaction becomes significant when the impacts of the main factors are not simply additive, but the impact of one factor depends on the level of the other factor. Further tested hypotheses about the decomposition of cellulose were: (4) Within one bog, there is no difference in mass loss between the three types of microhabitats (separate analyses for the Jizera Mts. and for the Jeseníky Mts.); and (5) Within one type of microhabitat, there is no difference in mass loss between the two environmentally contrasting bogs (three analyses for the microhabitats characterised by *Sphagnum* species).

The analyses of *Sphagnum* decomposition were even more structured. Besides the factor "environment of the decomposition site", two more factors were added: "species" and "origin of the material". First, the data were divided according to the locality of the material's origin, and the following null hypotheses were tested: (6) There is no difference in mass loss among the three *Sphagnum* species with respect to the environment of the decomposition site; (7) There is no difference in mass loss between the two decomposition sites with respect to the particular *Sphagnum* species; and (8) There is no significant interaction between the environment of the decomposition site and particular *Sphagnum* species. Second, the data on *Sphagnum* decomposition

were divided according to the decomposition site, and the following null hypotheses were tested: (9) There is no difference in mass loss among the three *Sphagnum* species with respect to the origin of the material; (10) There is no difference in mass loss between the two origins of the material with respect to the particular *Sphagnum* species; and (11) There is no significant interaction between the origin of the material and particular *Sphagnum* species. Third, the data were divided according to the *Sphagnum* species, and each data set was used to test the following null hypotheses: (12) There is no difference in mass loss between the two origins of the material with respect to the decomposition site; (13) There is no difference in mass loss between the two decomposition sites with respect to the origin of the material; and (14) There is no significant interaction between the origin of the material and the decomposition site. Tukey's HSD *post-hoc* test was performed to compare nutrient concentrations in *Sphagnum* tissues and N ions availability. Spearman's correlations were calculated between initial nutrient concentrations and losses of biomass and nutrients during decomposition. Unfortunately, not all bags could be found in the field (5 bags of *S. rubellum/russowii*, 6 bags of *S. magellanicum* and 14 bags of *S. fallax*); some of those could have been pulled out or destroyed by deer. Moreover, biomass left in some bags after the year was insufficient to be analysed individually for nutrient contents after the decomposition experiment. For these reasons, we decided to present the results concerning nutrient losses as follows: nutrient loss (%) = $(C_0W_0 - C_1W_1)/C_0W_0 \times 100$, where C_0 and C_1 are mean nutrient concentrations, and W_0 and W_1 are mean weights of *Sphagnum* biomass in the bags before (C_0 , W_0) and after (C_1 , W_1) one year of decay. Positive values indicate net mineralisation; negative values indicate net immobilisation (Bragazza *et al.* 2007). Statistical analyses were performed using Statistica for Windows (Statsoft Inc. 2011) and R (R Development Core Team 2012).

Results

Cellulose mass loss

Decomposition of cellulose differed between the

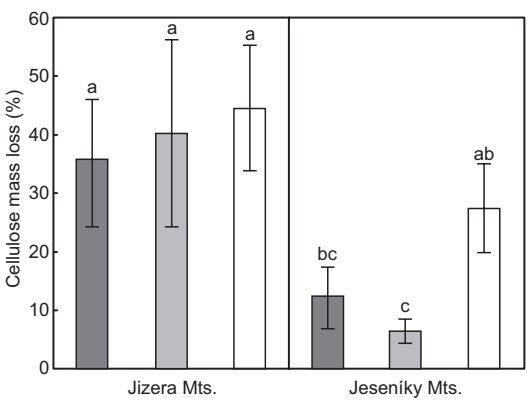


Fig. 2. Decomposition of cellulose (mass loss \pm SD) in the suboceanic Jizera and the subcontinental Jeseníky Mts. separately for microhabitats characterised by mono-dominant *Sphagnum* species, *S. rubellum/russowii* (black), *S. magellanicum* (grey), *S. fallax* (white). Decomposition experiment took one year. Different letters above the bars indicate significant ($p < 0.05$, Tukey's HSD) differences among *Sphagnum* species and between localities.

two regions (Jizera and Jeseníky Mts.) with higher cellulose mass loss in the warmer and more N-polluted Jizera Mts. (two-way ANOVA: $F_{1,35} = 10.7, p = 0.002$). Analogously, we found a higher mass loss of cellulose during decomposition in the Jizera Mts. when microhabitats of either *S. magellanicum* ($F_{1,12} = 6.3, p = 0.027$) or *S. rubellum/russowii* ($F_{1,11} = 5.1, p = 0.045$) were analysed separately. This difference was not significant for the microhabitat with *S. fallax*.

When we pooled the data from both regions, we found no difference in cellulose mass loss among microhabitats. On the other hand, we

found differences among the microhabitats within the subcontinental Jeseníky Mts. ($F_{2,18} = 4.5, p = 0.026$), where cellulose decomposed faster in the *S. fallax* microhabitat (average mass loss of 27.5%) than in the *S. magellanicum* microhabitat (average mass loss of 6.4%; Tukey's HSD: $p = 0.032$; Fig. 2).

***Sphagnum* mass loss**

We investigated *Sphagnum* mass loss with respect to locality of the material origin and decomposition site. We found significant differences in mass loss among species in both cases (Tables 1 and 2).

Tukey's HSD *post-hoc* test revealed that the mass of *S. magellanicum* decomposed less than the mass of other species in all combinations of material origin and decomposition site (see Tables 1 and 2); differences between *S. rubellum/russowii* and *S. fallax* were not significant. The effect of decomposition site on *Sphagnum* mass decomposition was statistically insignificant (see Tables 1 and 2).

In subsequent analyses of the effects of material origin and decomposition site on individual *Sphagnum* species, the only significant difference was found for *S. rubellum/russowii*, where the material originating from the subcontinental Jeseníky Mts. decomposed more than the material originating from the suboceanic Jizera Mts. (Table 3). Within particular study sites, *S. magellanicum* decomposed significantly less than *S. fallax* or *S. rubellum/russowii* (*S. russowii* in this case) in the Jeseníky Mts. (Fig. 3).

Table 1. Effects of the *Sphagnum* species and decomposition site on mass loss evaluated by two-way ANOVA separately for material originating from the suboceanic Jizera and the subcontinental Jeseníky Mts. *p* values set in boldface indicate significant effects.

Effect	Jizera Mts.		Jeseníky Mts.	
	<i>F</i> (df1,df2)	<i>p</i>	<i>F</i> (df1,df2)	<i>p</i>
Species	6.04 (2,8274)	0.004	5.32 (2,619)	0.007
Tukey's HSD	<i>magellanicum</i> vs. <i>fallax</i>	0.002	<i>magellanicum</i> vs. <i>rubellum/russowii</i>	0.01
Decomposition site	0.97 (1,74)	0.327	0.85 (1,69)	0.360
Species \times decomposition site	0.35 (2,74)	0.707	0.44 (2,69)	0.648

Nitrogen availability

In both study regions, the IER $\text{NH}_4^+\text{-N}$ values were significantly higher than the IER $\text{NO}_3^-\text{-N}$ values. This result was obtained for pooled data from all microhabitats (two-way ANOVA: $F_{1,416} = 558.5$, $p < 0.001$) as well as for particular microhabitats analysed separately ($F_{1,146} = 220.2$, $p < 0.001$ for *S. rubellum/russowii*; $F_{1,136} = 192.0$, $p < 0.001$ for *S. magellanicum*; $F_{1,130} = 201.9$, $p < 0.001$ for *S. fallax*; Fig. 4). Comparing study sites, we unexpectedly found slightly higher concentrations of IER ammonium in the suboceanic Jizera Mts. ($F_{1,203} = 0.1$, $p = 0.730$) while the concentrations of IER nitrate ($F_{1,203} = 4.5$, $p = 0.035$) were higher in the subcontinental Jeseníky Mts, which does not correspond to higher N deposition in the suboceanic Jizera Mts. We found higher N availability during winter as compared with that during the vegetation period in the suboceanic Jizera Mts. ($F_{1,108} = 18.8$, $p < 0.001$ for ammonium ions; $F_{1,108} = 5.4$, $p = 0.022$ for nitrate ions). By contrast, in the subcontinental Jeseníky Mts, IER ammonium concentrations were relatively constant ($F_{1,97} = 0.2$, $p = 0.625$), and nitrate concentrations were not ($F_{1,97} = 9.0$,

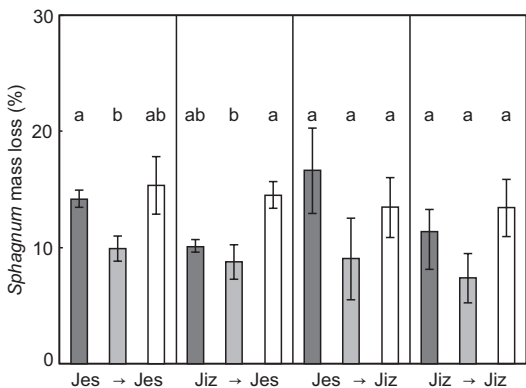


Fig. 3. Decomposition of *Sphagnum* species (mean \pm SE) with respect to the origin of the material and decomposition sites, the suboceanic Jizera Mts. (Jiz) and the subcontinental Jeseníky Mts. (Jes); the arrows indicate the direction of transplant from the site of the material origin to the decomposition site. *S. rubellum/russowii* (black), *S. magellanicum* (grey) and *S. fallax* (white) are categorised according to the origin of the material and the decomposition site. The decomposition experiment took one year. Different letters above the bars denote significant differences among *Sphagnum* species in the relevant category.

$p = 0.003$). Among the microhabitats formed by particular *Sphagnum* species, both more ammo-

Table 2. Effects of *Sphagnum* species and the origin of the material on mass loss evaluated by two-way ANOVA separately for decomposition site, the suboceanic Jizera and the subcontinental Jeseníky Mts. p values set in boldface indicate significant effects.

Effect	Jizera Mts.		Jeseníky Mts.	
	<i>F</i> (df1,df2)	<i>p</i>	<i>F</i> (df1,df2)	<i>p</i>
Species	4.29 (2,7482)	0.017	8.63 (2,691)	< 0.001
Tukey's HSD	<i>magellanicum</i> vs. <i>rubellum/russowii</i>	0.028	<i>magellanicum</i> vs. <i>rubellum/russowii</i>	0.029
	<i>magellanicum</i> vs. <i>fallax</i>	0.047	<i>magellanicum</i> vs. <i>fallax</i>	< 0.001
Material origin	0.91 (1,82)	0.343	3.48 (1,61)	0.066
Species \times material origin	0.38 (2,82)	0.686	0.87 (2,61)	0.422

Table 3. Effects of the origin of the material and the decomposition site separately for *S. rubellum/russowii*, *S. magellanicum* and *S. fallax* evaluated by two-way ANOVA. p value set in boldface indicate significant effect.

Effect	<i>S. rubellum/russowii</i>		<i>S. magellanicum</i>		<i>S. fallax</i>	
	<i>F</i> (df1,df2)	<i>p</i>	<i>F</i> (df1,df2)	<i>p</i>	<i>F</i> (df1,df2)	<i>p</i>
Material origin	6.44 (1,51)	0.014	0.39 (1,50)	0.533	0.04 (1,42)	0.844
Decomposition site	0.06 (1,51)	0.808	1.54 (1,50)	0.220	1.17 (1,42)	0.286
Material origin \times decomposition site	0 (1,51)	0.956	0.03 (1,50)	0.870	0 (1,42)	0.991

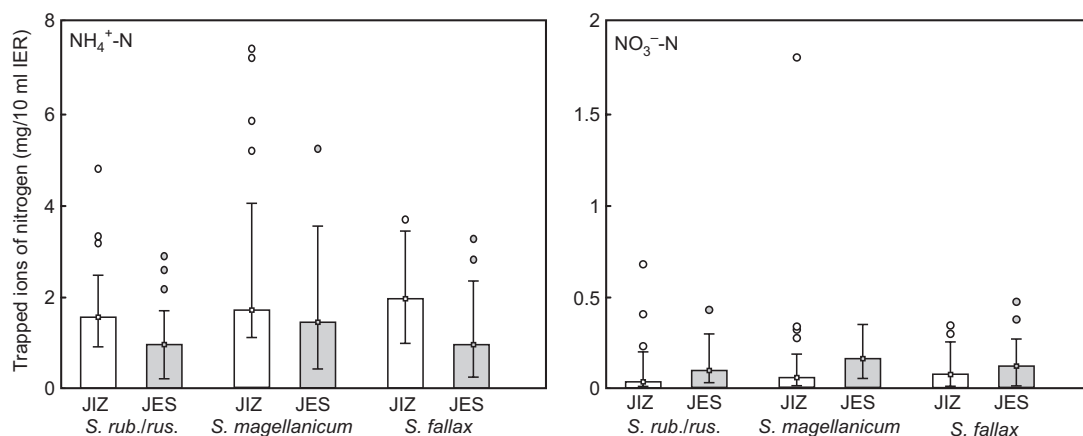


Fig. 4. Median available ammonium (NH_4^+) and nitrate (NO_3^-) ions trapped *in situ* by ion-exchange resins stockings (IER). Whiskers indicate the range within 1.5 times the length of distribution between 25 and 75 percentiles. Values outside this range are indicated by open circles.

nium ($F_{2,203} = 8.3$, $p < 0.001$) and more nitrate ions ($F_{2,203} = 1.8$, $p = 0.163$) were captured in the *S. magellanicum* microhabitats than in the *S. fallax* (*post-hoc* test for ammonium ions, $p = 0.014$) and *S. rubellum/russowii* microhabitats (*post-hoc* test for ammonium ions; $p < 0.001$).

Initial nutrient concentrations in *Sphagnum* biomass and nutrient loss during decomposition

We found higher tissue nutrient concentrations in the subcontinental Jeseníky Mts. (significantly P, K and Mg; regardless of the species) than in the suboceanic Jizera Mts, and generally for *S. fallax* (significantly K; without respect to the origin of the material). By contrast, C, Ca and N concentrations in *Sphagnum* biomass did not vary significantly across all species and localities (Table 4). In addition, concentrations of P, K, Ca and Mg correlated significantly.

K was most quickly released during the decomposition experiment, followed by P, and then by N, Ca and Mg (Fig. 5). In the case of Ca and Mg, we frequently observed higher concentrations in the *Sphagnum* material after the decomposition experiment than the initial concentration. There were only minor differences in C loss, but the lowest C loss in *S. magellanicum* was related to the lowest mass loss of this species as compared with the others (Fig. 3). K, P and Ca

concentrations determined before the decomposition experiment correlated significantly positively with N loss during the decomposition experiment. In addition, C loss correlated significantly positively with Ca concentrations, and Mg loss with Mg concentrations. Among all the tested nutrients (N, P, K, Ca and Mg), *Sphagnum* mass loss correlated significantly only with initial Ca concentrations (Table 5).

Discussion

Decomposition of cellulose and *Sphagnum* biomass in warmer and nitrogen-rich conditions

We found faster decay of cellulose in the suboceanic Jizera Mts., where higher temperatures and higher atmospheric N deposition occur as compared with the subcontinental Jeseníky Mts. Our results on cellulose decomposition indicate that, although the separate effects of temperature and N deposition could not be disentangled in our study, the environment of the decomposition sites influenced decomposition rates. Furthermore, we found the highest cellulose decay rates in the *S. fallax* microhabitat, which is characterised by higher nutrient availability (N, P, K, Ca and Mg). The high nutrient availability may have caused C:N, C:P and other C ratios to decrease, enhancing microbial decomposition (Kuhry and

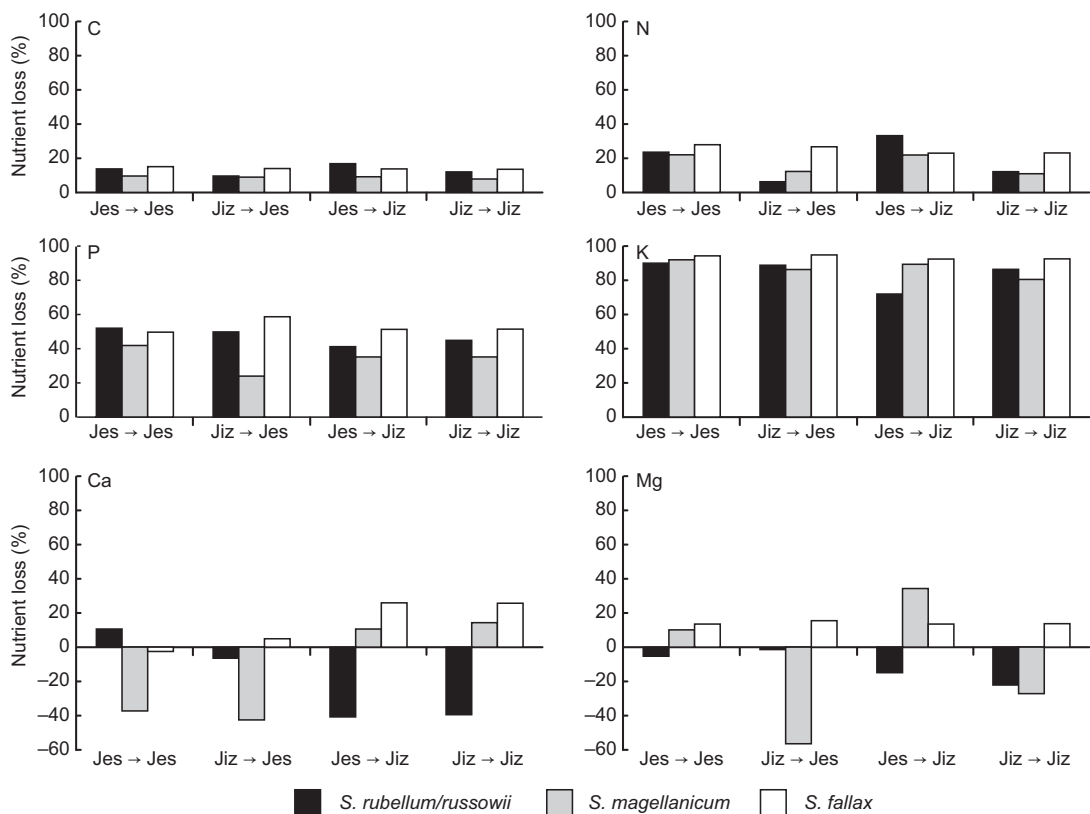


Fig. 5. Mean nutrient loss (%) from *Sphagnum* biomass after one year of decomposition. Negative values of nutrient loss indicate immobilisation in biomass during decomposition experiment. Jiz = suboceanic Jizera Mts., Jes = subcontinental Jeseníky Mts.; the arrows indicate the direction of transplant from the site of the material origin to the decomposition site.

Vitt 1996, Limpens and Berendse 2003, Bra-gazza *et al.* 2006, Thormann 2006, Gerdol *et al.* 2007).

Contrary to the cellulose test, we did not find significant differences between original and transplanted *Sphagnum* material as well as

Table 4. Initial nutrient concentrations (mg g⁻¹, mean ± SE) in *Sphagnum* stems from the suboceanic Jizera and the subcontinental Jeseníky Mts. Different letters indicate significant differences within columns (Tukey's HSD: *p* < 0.05).

<i>Sphagnum</i> species and their origin	N	P	K	Ca	Mg	C
<i>S. rubellum/russowii</i>						
Jizera	8.6 ± 0.6 ^a	0.38 ± 0.02 ^b	1.5 ± 0.1 ^b	2.4 ± 0.1 ^a	0.6 ± 0.1 ^{bc}	489.9 ± 0.1 ^a
Jeseníky	8.7 ± 0.8 ^a	0.54 ± 0.05 ^{ab}	4.2 ± 0.4 ^a	3.1 ± 0.2 ^a	0.9 ± 0.1 ^{ab}	487.2 ± 0.2 ^a
<i>S. magellanicum</i>						
Jizera	10.6 ± 0.3 ^a	0.48 ± 0.04 ^{ab}	1.6 ± 0.3 ^b	2.7 ± 0.2 ^a	0.6 ± 0.1 ^c	486.1 ± 0.1 ^a
Jeseníky	10.1 ± 0.4 ^a	0.52 ± 0.04 ^{ab}	4.2 ± 0.2 ^a	2.9 ± 0.2 ^a	1.1 ± 0.0 ^a	487.6 ± 0.0 ^a
<i>S. fallax</i>						
Jizera	10.3 ± 0.4 ^a	0.48 ± 0.06 ^{ab}	4.1 ± 0.6 ^a	3.1 ± 0.4 ^a	0.8 ± 0.1 ^{abc}	489.1 ± 0.1 ^a
Jeseníky	9.7 ± 0.1 ^a	0.63 ± 0.05 ^a	6.3 ± 1.2 ^a	3.3 ± 0.3 ^a	1.1 ± 0.1 ^a	486.1 ± 0.7 ^a

between the contrasting environmental conditions at the decomposition sites during the experiment. In accordance with earlier studies (Johnson and Damman 1991, Belyea 1996, Limpens and Berendse 2003, Straková *et al.* 2011), our study showed that differences in the intrinsic properties of the biomass of each *Sphagnum* species override the effects of material origin as well as decomposition site. In the case of *S. rubellum/russowii* only, material collected from the subcontinental Jeseníky Mts. decomposed significantly faster than material from the suboceanic Jizera Mts. However, these results have to be treated with caution, as the material from the two origins also differs taxonomically. *Sphagnum rubellum* occurs in the Jizera Mts. whereas *S. russowii* occurs in the Jeseníky Mts.

The discrepancy between cellulose and *Sphagnum* mass loss confirms that higher temperatures and N deposition seem to be insufficient at altering the abundance of microorganisms decomposing polyphenols in sphagna to an extent that influences decomposition rates, at least during the one-year study period. Previous studies (Moore *et al.* 2007, 2008) demonstrated that short-term assessments of decomposition rates may not be necessarily related to longer-term patterns. Results concerning initial mass loss can be biased towards species-identity controls, while longer-term experiments capture more of environmental variation. Nevertheless, local environmental conditions seem to be more important when comparing contrasting wetland environments such as birch forests with mires (Lang *et al.* 2009), minerotrophic versus ombrotrophic mires (Bragazza *et al.* 2007) or drained versus natural mires (Liefers 1988).

Nitrogen uptake in conditions of high N deposition

Our data from the ion-exchange resin analysis demonstrate differences in peat N availability between the two study regions (generally slightly higher IER ammonium in the Jizera Mts.) and partly also among the *Sphagnum* species (Fig. 4). Higher ammonium availability in the Jizera Mts. is very likely a consequence of higher atmospheric N deposition in combination with a more positive balance between production and consumption of ammonium ions (between ammonization and immobilization) due to warmer suboceanic climate conditions there. Concerning nitrate availability, Francez *et al.* (2011) evaluated the impact of increasing N inputs on denitrification rates beneath the *S. magellanicum* layer. As a consequence of increasing levels of N deposition, higher amounts of mineral N reach the underlying peat layer, modifying its N sink capacity via denitrification (Francez *et al.* 2011). By analogy, the lower IER nitrate levels in the suboceanic Jizera Mts. probably reflect a lower N sink capacity caused by elevated denitrification activity. The higher microbial activity (ammonization and denitrification) under the warmer suboceanic climate conditions of the Jizera Mts. follow the same pattern as the higher cellulose decomposition (*see* Fig. 2).

The critical N load for *Sphagnum* growth, previously recommended by Bobbink *et al.* (1996) (0.5–1.0 g m⁻² yr⁻¹), was latter described as reliable (Bobbink *et al.* 2003). Additionally Vitt *et al.* (2003) found out for net primary production of *Sphagnum* species a critical N-deposition value of between 1.48 and 1.57 g m⁻² yr⁻¹, and Xing

Table 5. Correlation matrix (Spearman's correlation coefficients) between initial nutrient concentrations and their losses in *Sphagnum* biomass during the decomposition experiment. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; n.s. = not significant.

	N loss (n = 12)	P loss (n = 12)	K loss (n = 12)	Ca loss (n = 12)	Mg loss (n = 12)	C loss (n = 12)	Mass loss (n = 51)
N conc.	-0.07 ^{n.s.}	-0.30 ^{n.s.}	0.16 ^{n.s.}	0.21 ^{n.s.}	0.03 ^{n.s.}	-0.47 ^{n.s.}	-0.07 ^{n.s.}
P conc.	0.74**	0.22 ^{n.s.}	0.35 ^{n.s.}	0.27 ^{n.s.}	0.32 ^{n.s.}	0.57 ^{n.s.}	0.24 ^{n.s.}
K conc.	0.75**	0.29 ^{n.s.}	0.50 ^{n.s.}	0.32 ^{n.s.}	0.52 ^{n.s.}	0.57 ^{n.s.}	0.23 ^{n.s.}
Ca conc.	0.89***	0.52 ^{n.s.}	0.55 ^{n.s.}	0.40 ^{n.s.}	0.45 ^{n.s.}	0.78**	0.43**
Mg conc.	0.52 ^{n.s.}	0.24 ^{n.s.}	0.47 ^{n.s.}	0.20 ^{n.s.}	0.68*	0.38 ^{n.s.}	0.21 ^{n.s.}

et al. (2011) specified a similar threshold for N retention capacity in northern peatlands ($1.6 \text{ g m}^{-2} \text{ yr}^{-1}$). The rate of N deposition in the experimental study region in the Jizera Mts. exceeded the above-mentioned threshold values (about $2\text{--}2.5 \text{ g m}^{-2} \text{ yr}^{-1}$). In the Jeseníky Mts, the rate of N deposition was very close to these thresholds (about $1.25 \text{ g m}^{-2} \text{ yr}^{-1}$). However, there is growing awareness that unacceptable habitat changes may not only be caused by exceedance of the critical load, but that they can also be derived from short-term exposure to high N concentrations (Pearce and van der Wal 2008). Nevertheless, current critical loads for peatlands are likely to hold under the future climate even though the predicted impacts of likely changes in N deposition on *Sphagnum* appear to be less severe than those of the climate (Granath *et al.* 2014).

The low uptake rate of N by *S. magellanicum* revealed by our IER analysis is consistent with the finding of Jauhiainen *et al.* (1998), who compared intracellular uptake of NH_4^+ and NO_3^- in seven *Sphagnum* species. The low ability of *S. magellanicum* to compete for N probably leads to its competitive exclusion by other faster-growing *Sphagnum* species like *S. fallax* (Twenhöven 1992, Hájek and Adamec 2009). Limpens *et al.* (2003) hypothesised that *S. fallax* can dominate if the N concentration in the *Sphagnum* capitula reaches at least 7 mg g^{-1} and the P concentration reaches at least 0.7 mg g^{-1} , which are values corresponding to N-polluted central-European subcontinental summit bogs. In the previous study, Jiroušek *et al.* (2011) found that the growth of *S. fallax* in the suboceanic Jizera Mts. still seems to be P-limited. In the subcontinental bogs of the Jeseníky Mts., by contrast, higher P availability may allow its expansion. Similarly, Granath *et al.* (2012) found that the future expansion of fast-growing species like *S. fallax* under elevated N conditions may depend on P availability.

Nutrient stoichiometry and losses

Nitrogen concentration in *Sphagnum* biomass did not correlate with atmospheric N deposition, which corresponds with larger data set collected by Jiroušek *et al.* (2011). Under high N

deposition, mosses become saturated by nitrogen unless availability of other nutrients increases and no longer uptake superfluous nitrogen (Bragazza *et al.* 2004), but this is probably not our case (*see below*). Besides N uptake, biomass N concentration can be affected by species-specific physiological processes (Harmens *et al.* 2011). Other possible factors are the dilution effect, which possibly takes place in the more biomass producing *S. fallax* and *S. rubellum/russowii* (Fritz *et al.* 2012), and the ability of *Sphagnum* mosses to detoxify excess N (Fritz *et al.* 2014).

Unlike Breeuwer *et al.* (2008), we did not find any relationship between N concentration in *Sphagnum* biomass and N loss during field decomposition experiment (Table 5), which could be caused by microbial immobilisation. Alternatively, Breeuwer *et al.* (2008) used different species (*S. fuscum* and *S. balticum*) and also found much lower N concentrations in *Sphagnum* stems and capitula, ranging from 3 to 8 mg g^{-1} , in contrast to our study where N concentrations of *Sphagnum* stems were higher and ranged from 8 to 11 mg g^{-1} . In both regions under study, atmospheric N deposition was probably too high to be absorbed by *Sphagnum* tissues (Bragazza *et al.* 2004). In such cases, the bog environment tends to become N-oversupplied, so its productivity becomes limited by other nutrients, especially P (Wang and Moore 2014). Hogg *et al.* (1994) found that the decomposition of *S. magellanicum* biomass is influenced more by P than by N. We found the N:P ratio in the *Sphagnum* biomass to be about 17 in the subcontinental bog in the Jeseníky Mts, which corresponds to the previous study of Jiroušek *et al.* (2011). The N:P ratio of about 22 found in the suboceanic Jizera Mts. is lower as compared with that reported in the previous study of Jiroušek *et al.* (2011; the N:P ratio for the same locality measured in 2006 was 28.57), which may be explained by decreased N deposition between 2006 and 2008. Based on the threshold N:P ratio of about 30 for continuing *Sphagnum* growth under increasing N deposition (Bragazza *et al.* 2004), we could argue that N seems to be still the limiting nutrient even in the case of the Jeseníky Mts. (Jiroušek *et al.* 2011) despite high atmospheric N deposition.

In our study, we hypothesized that higher initial nutrient concentrations in the biomass would

cause higher mass loss. Initial P, K, Ca and Mg concentration, but only Ca concentration significantly, were positively correlated with the total mass loss (Table 5). The similar result for K, but not for Ca, was already reported by Lang *et al.* (2009). On the other hand, Ivarson (1977) found higher decomposition of *Sphagnum* peat after CaCO_3 and MgCO_3 addition. We further found K to show the highest release during the decomposition, corroborating the results of Bragazza *et al.* (2007, 2008). Because K leaching occurs easily, it is rather difficult to distinguish between the effects of physical leaching and microbial activity; however, they are probably connected (Limpens and Berendse 2003). It is also important to note that both high initial K concentration and high K loss were specific for the most rapidly decomposing *S. fallax*, making it impossible to generalise the patterns found for K.

Differences in decomposition among *Sphagnum* species

We hypothesized that *S. fallax* (sect. *Cuspidata*) would decompose faster than *S. magellanicum* (sect. *Sphagnum*) and that *S. rubellum/russowii* (sect. *Acutifolia*) would decompose the slowest. However, this hypothesis turned out to be true only in the case of *S. fallax*, which decomposed the fastest in all treatments, except for material originating from the subcontinental Jeseníky Mts. that was incubated in the suboceanic Jizera Mts. Surprisingly, we found a lower mass loss of *S. magellanicum* as compared with that of *S. rubellum/russowii*. These interspecific differences can generally be explained by C allocation strategies of these species (Turetsky *et al.* 2008, Hájek *et al.* 2011). Species avoiding water stress (typically *S. magellanicum* or *S. rubellum* rather than *S. russowii*) invest relatively more C into structural, water holding tissues consisting of dead cells than their competitors (species from the sect. *Cuspidata* or *S. russowii* rather than *S. rubellum*) that allocate more C to photosynthesis and growth (i.e., metabolically active tissue that is rich in mineral nutrients and less recalcitrant C). Competitors are therefore more efficient in nutrient uptake and utilization, and become competitively successful under reduced stress.

Interspecific differences may also explain the sole statistically significant effect of material origin (Table 3). Although *Sphagnum rubellum* and *S. russowii* are taxonomically allied species (*S. rubellum* is probably a parent of *S. russowii*; Shaw *et al.* 2005), belonging to the same section and even forming morphologically transitional populations, *Sphagnum rubellum* (collected in the suboceanic Jizera Mts.) decomposed more slowly than *S. russowii* collected in the subcontinental Jeseníky Mts. Note that for the other two species there was no difference in decomposition between material originating at different localities. This result suggests that interspecific differences, independent of environmental effects, may hold also for closely related and sympatrically occurring species. It, moreover, suggests that it may not be appropriate to consider *Sphagnum* species from the same section as a single homogeneous entity in studies of ecosystem functioning and the effects of global changes. Although *S. russowii* is one of the dominant *Sphagnum* species in subcontinental European summit bogs (Bragazza *et al.* 2005b, Hájková *et al.* 2006, 2010), it is not included in analogous studies from Scandinavia or North America, where this species occurs in more minerotrophic environments (Gignac and Vitt 1990, Laine *et al.* 2009).

Interconnection between ecosystem functioning and vegetation change

Our finding that in highly polluted summit bogs, interspecific differences govern *Sphagnum* decomposition patterns, inherently affecting C and nutrient cycling, may have crucial consequences for ecosystem change predictions. Many species have recently changed their frequencies in bogs (Gunnarsson *et al.* 2002, Hájková *et al.* 2011, Kapfer *et al.* 2011), and this change has an ecophysiological background. Previously, Press *et al.* (1986) pointed out that some *Sphagnum* species are more sensitive to atmospheric pollution than others. In a more recent study, Wiedermann *et al.* (2009) suggested that *S. balticum* is more sensitive than *S. fuscum* to high N supply. Analogously, our data from the ion-exchange resin analysis demonstrate that *S. magellanicum* is unable to take advantage of higher mineral

N availability as effectively as *S. fallax* and *S. rubellum/russowii* under high N deposition load.

Considering the causality of relationships concerning N deposition, species-specific responses to it, ongoing vegetation change and decomposition patterns, we can integrate the results of this study with those already available from the same bogs (Jiroušek *et al.* 2011, Hájková *et al.* 2011, Dudová *et al.* 2013). This can further our understanding of ecosystem functioning and improve predictions of future development. The gradual replacement of *S. magellanicum* by the other *Sphagnum* species has been confirmed by a permanent-plot study from the same regions, the Jizera Mts. and the Jeseníky Mts. (Hájková *et al.* 2011). In the subcontinental Jeseníky Mts., the frequency of *S. magellanicum* in permanent plots in hummocks and lawns decreased from 40% in 1991 to 7% in 2008. On the other hand, *Sphagnum* species from sect. *Cuspidata* slightly increased in both study regions (Hájková *et al.* 2011) despite the slightly decreasing water table. At the Holocene scale, Dudová *et al.* (2013) found that *S. russowii* rather recently replaced *S. magellanicum* in the peat sediment, but exact dating of this event was impossible because of a hiatus in the palaeoecological record separating *S. magellanicum* and *S. russowii* phases. Nevertheless, this hiatus is probably caused either by increasing human intervention in the bog or a drier climate (Dudová *et al.* 2013). This change of species composition could therefore lead to a change in decomposition rates and hence C cycling, but more focused long-term research is needed.

Conclusions

We found faster decay of cellulose in summit bogs in the warmer and highly N-polluted suboceanic Jizera Mts. as compared with that in the subcontinental Jeseníky Mts. However, because of the specificity of decomposers, it is impossible to generalise this result to *Sphagnum* decomposition. In the case of *Sphagnum* decomposition, interspecific differences outweighed the effects of both the origin of the material and the environment of the decomposition site. *S. magellanicum* decomposed more slowly than both *S. russowii* and *S. fallax*, the species which

gradually replace it in summit bogs of the Czech Republic. We conclude that (i) taxonomic identity should be carefully taken into account in large-scale studies and meta-analyses focused on *Sphagnum* decomposition patterns, and that (ii) the relationships between nutrients in the environment and the competitive force of more nutrient-demanding *Sphagnum* species may lead to vegetation changes in moss layers, and with respect to species-specific mass loss, indirectly to shifts in decomposition rates in N-polluted areas. Any changes in *Sphagnum* species composition should therefore be considered when predicting future nutrient cycling in bogs.

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